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STATE COLLEGE OF WASHINGTON
AGRICULTURAL EXPERIMENT STATION
Pullman, Washington

Division of Agronomy

IMPERIAL MYCOLOGICAL INSTITUTE
19 MAR. 1936

Wheat Inheritance: Reaction to Four Bunt Biotypes, Spike Density, and Seed Color

by

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Bulletin No. 323
(Technical Paper)
December, 1935

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WHEAT INHERITANCE: REACTION TO FOUR BUNT BIOTYPES, SPIKE DENSITY, AND SEED COLOR

A. M. Schlehuber[1]

INTRODUCTION

Breeding for resistance to disease is carried on by almost all experiment stations. Similar diseases do not have the same relative importance in different sections of the country, however. For instance, in the Great Plains area, kernel smut of sorghum, *Sphacelotheca sorghi* (Lk.) Cl. and bunt of wheat, *Tilletia tritici* (Bjerk.) Wint. and *T. levis* Kühn, can be controlled by properly treating the seed with copper carbonate. Naturally, breeding for resistance to these two diseases is a minor problem as compared to breeding for other desirable qualities. Here the plant breeders can concentrate on the development of qualities of more relative importance. In the Pacific Northwest, however, where bunt in winter wheat can merely be checked but cannot be controlled effectively by seed treatment, the breeding of varieties resistant to this disease is a problem of major importance.

In order to proceed most intelligently in a breeding program of disease resistance, it is helpful to have a knowledge of the qualities of the parents pertaining to resistance. Salmon and Laude (39)[2] state that "the random crossing of varieties to induce variation or in the hope of securing favorable chance combinations is too uncertain a method on which to base a crop-improvement program." The writer suggests that a more satisfactory method of obtaining the desirable progeny is found by using an extremely large number of progeny from a few thoroughly studied parents, thereby increasing the possibilities of recombination of the desirable factors.

The inheritance of resistance of two winter wheat crosses to four physiologic forms of bunt is discussed in the earlier part of this paper; the latter part deals with inheritance studies of spike density and seed color.

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[2] Figures in parenthesis refer to "Literature Cited," p. 30.

HISTORICAL RESUME

Bunt Resistance

Farrer, in 1901, according to Briggs (5) seems to have been the first to attempt to bring about bunt resistance in wheats by hybridization. Two varieties, Florence and Genoa, which are highly resistant, were produced. Briggs (5) in 1926 states, "Gaines seems to have made the only attempt to investigate the genetics of resistance to bunt."

Reed (36) made a rather thorough review of the literature pertaining to varietal resistance to bunt in 1924. He concluded that soil moisture, soil temperature, and other possible soil conditions are independent factors which determine the occurrence of bunt in wheat, and that their interaction determines whether or not infection will take place and also the severity of the attack. Tisdale et al. (52) made a very comprehensive report of the relative resistance of wheat varieties to bunt in the Pacific Coast states.

The presence of physiologic races has been demonstrated by Rodenhiser and Stakman (38), Gaines (24), Reed (37), and Bressman (4). It is obvious that this condition complicates the program of breeding commercial varieties resistant to bunt.

Gaines (19) made a study of the comparative smut resistance of Washington wheats. It was his opinion that there are two distinct conditions that control the resistance of wheat to smut—one preventing infection, the other preventing smut-balls from forming. In 1920 Gaines presented data on the bunt resistance of three wheats, Turkey (Washington No. 326), Hybrid 128 (Washington No. 592), and Florence (Washington No. 634), and the resistance of the F_2 and F_3 of two crosses, Turkey x Hybrid 128 and Turkey x Florence. The F_2 and F_3 of Turkey x Florence produced a much higher degree of bunt than either parent. It was suggested that most of the factors for resistance are recessive, and Turkey and Florence each have different and distinct factors for resistance. A continuous series ranging from complete immunity to complete susceptibility was obtained from which it was concluded that resistance, if Mendelian, is composed of multiple factors. In later studies by Gaines (21, 22), multiple factors were thought to govern resistance. In a Marquis x Turkey cross, Gaines and Singleton (23) suggested two factors for resistance, one being carried by each parent and the Turkey factor being the most "prepotent."

Gieseke (26) and Knorr (34) in Germany concluded that immunity was inherited as a recessive and governed by multiple factors. Aamodt (1) thought that resistance was controlled by multiple factors.

Briggs (5, 6, 7, 8, 9, 10) and Churchward (11, 12) each report that resistance is controlled by one factor.

The exact nature of resistance is not known. It is known, however, that certain environmental factors play an important part in the amount of infection in the following crop. Hungerford (33), on the basis of greenhouse experiments, demonstrated that low soil temperatures and a fairly high percentage of moisture in the soil are both conducive to stinking smut infection. Smith (41) studied the relation between temperature and reaction to bunt at different stages of growth for Hope and Jenkin in the greenhouse. Hope was resistant when grown at a relatively low temperature until emergence from the soil and then grown at a higher temperature, although plants grown continuously in the cool environment were quite susceptible. Smith suggests that "the resistance of Hope at the higher temperature is dependent upon either unfavorable nutritional conditions or an organization of the protoplasm that at this temperature retards or inhibits the growth of the fungus."

Giljarovskij and Zak in 1930, according to Von Rathlef (53) studied the correlation between rate of growth, degree of acidity, and osmotic pressure of the cell sap and the susceptibility to bunt in certain *Triticum vulgare* and *T. durum* types. They found that resistance increased with an increase in rate of growth, with a shift of the pH of the cell sap towards the alkaline side, and with an increase of osmotic pressure. The *durum* forms in general have a higher pH value and a stronger osmotic pressure than the *vulgare* forms, and through this was explained their greater resistance in general. Hurd-Karrer (32), however, in an experiment of the relative titratable-acid concentration of the juices of 12 varieties, concluded there was no causal relation between a higher concentration of hydrogen ions in the juice and resistance to *Tilletia tritici*.

The effect of bunt on yield of wheat has been studied recently by Flor, Gaines, and Smith (16). It was found that yield is roughly inversely proportional to percentage of bunted heads. Heald and Gaines (30) found a correlation coefficient of $-.713 \pm .045$ between smut and yield.

Spike Density

In general, simple segregation has been observed in genetic studies of spike density. Biffen (2) and Gaines (18) each report ratios explained by assuming a one-factor difference. Nilsson-Ehle in 1911, according to Hayes and Garber (28), studied crosses between compact and middense wheats. The F_2 segregated into compact, middense, and lax forms. He assumed that the dense form was of the composition $CCL_1L_1L_2L_2$. The C factor was thought to inhibit the expression of the lengthening factors L_1 and L_2 and also to produce spikes with short internodes. Wilson (54) reported a 3:1 ratio in a Red King x Rood Korean cross. Parker (35) in a *Triticum compactum* x *T. vulgare* cross was able to demonstrate segregation but found the condition was complex. Boshnakian (3) obtained ratios which approached 3 dense :

1 lax. The F_3 showed various degrees of density within the dense and lax forms. Boshnakian thought that different density factors form an allelomorphic series, and that these factors belong to a multiple series. Florell (17) suggested a one-factor difference between club and lax types of spike. In the F_3 generation he was able to segregate both club and lax segregates of different densities. Stewart (45) reported results similar to those of Florell. He obtained a close approximation to a 1:2:1 ratio of dense, intermediate, and lax spikes, and in each three major groups there was a series of smaller differences in spike density. Stewart (46), Stewart and Heywood (47), Stewart and Price (48), Stewart and Woodward (49), Stewart and Bischoff (50), and Stewart and Dalley (51) report segregation of spike density into simple 1:2:1 ratios.

Seed Color

Biffen (2) reported segregation into 3 red : 1 white between red and white seeded wheats. According to Hayes and Garber (28), Nilsson-Ehle was the first investigator to report crosses which in F_3 gave 3:1, 15:1, and 63:1 ratios of red to white seeded plants. The Howards (31) in India, Gaines (18), Stewart (46), and Stewart and Woodward (49) report segregation approximating 63:1 ratios.

Hayes and Robertson (29) gave results which indicate that the red color in Marquis is the result of two independently inherited factors, either one of which alone leads to the production of red color. Stewart and Dalley (51) suggest a two-factor difference in a cross involving Utac and Ridit.

MATERIALS

Albit (*Triticum compactum humboldtii* Koern.) C. I.[1] 8275 is described by Clark, Parker, and Waldron (14), and its commercial importance by Gaines and Schafer (25). It is a club wheat with awnless spikes, glabrous white glumes, and soft white kernels. It is used as one of the parents in both winter wheat crosses. Minhardi (*Triticum vulgare lutescens* Al.) C. I. 5149 is described by Clark and Bayles (13). It is a wheat belonging to the class Soft Red Winter, and possesses awnless spikes and glabrous white glumes. Clark and Bayles state, "It is one of the most winterhardy wheats grown." Buffum 17 (*T. vulgare lutescens* Al.) C. I. 3330 is a soft red winter wheat similar to Minhardi in appearance. This variety also possesses unusual winter hardiness.

Four physiologic forms or biotypes of bunt—T-1[2], T-2[2], T-13[2], and L-5[3]—were used for inoculum in these smut tests. T-1 is the old Pullman form that has been used in smut tests at this station since 1914. T-2 and L-5 were collected at Waterville, Washington in 1929. These

[1] Refers to U.S.D.A. accession number of Cereal Investigations.
[2] Forms belonging to **Tilletia tritici**.
[3] A form belonging to **T. levis**.

three have been recognized by Heald and Gaines (30) as distinct forms. T-13, since then recognized as a distinct form, was sent in by Bressman of Corvallis, Oregon, and was first used in the Pullman physiologic form nursery in 1930. These biotypes have been kept pure by culturing on differential hosts. By referring to Table 1 it can be seen that Hussar and Martin differentiate biotypes T-1 and T-2, but not T-2 and T-13. Up to the present time no winter wheat tested at this station has satisfactorily differentiated the two latter forms. The spring wheats, in general, are unsatisfactory as differential hosts. However, there is one, Dreger's Spring, C. I. 11493, that differentiates between forms T-2 and T-13 (Table 1). L-5 can be distinguished from forms T-1, T-2, and T-13 by the use of the microscope. Smith (42) described and illustrated methods for distinguishing T-2 from T-3 on Martin wheat by the appearance of the bunted spikes. The use of differential host testers has been the method employed at the Washington station to maintain the purity of physiologic forms.

Table 1. Reaction of Varieties of Wheat Used as Differential Hosts

Variety	Year of test	Per cent bunt			
		T-1	T-2	T-13	L-5
Hussar	1930	0	60	50	0
Martin	1930	0	37	55	0
Dreger's Spring	1931	0	0	20	10

METHODS

The F_1 and F_2 of the crosses Albit x Minhardi and Albit x Buffum 17 were treated with copper carbonate before planting to protect them as much as possible from smut infection. In the summer of 1931, 301 Albit x Minhardi F_2 plants and 202 Albit x Buffum 17 F_2 plants were collected for future inheritance studies. After notes on seed color and measurements of spike density were taken, the seed of each F_2 plant was divided into five different portions of 75 seeds each. The planting plan may be summarized as follows:

Inoculum	No. of progenies, each represented by a rod row of 75 seeds			
	Parents	Albit x Minhardi F_3	Parents	Albit x Buffum 17 F_3
0	30	145	24	104
T-1	32	150	22	102
L-5	28	131	22	95
T-13	26	119	18	84
T-2	24	111	18	75

In addition, 23 seeds of Albit x Minhardi F_1 and 20 of Albit x Buffum 17 F_1 were inoculated with T-1 in order to get an indication of dominance.

The seed was inoculated by placing in a glass vial the different portions of 75 seeds and a sufficient quantity of fresh viable bunt spores gathered from the last crop from varieties showing reliable differentiation for these forms; these were shaken vigorously until all seeds were thoroughly blackened with spores.

Planting was done entirely by hand, in rows one rod long and 18 inches apart, the seeds being spaced from two to three inches apart to insure separation of individual plants. Ten rows of progeny were planted after one row of each of the parents. The planting was completed in three days, thus making the experiment as uniform as possible.

The nursery had been in wheat and summer fallow, respectively, the two previous seasons.

At the time of planting, the soil was somewhat deficient in moisture; consequently, germination was poor. Rather severe winter conditions, winter-killing a few plants, in addition to the poor germination, resulted in a few of the progenies having numbers too low for a satisfactory analysis.

Shortly before maturity (soft-dough stage) all plants were classified into lots according to the percentage of smut. All plants containing smut were pulled and put in their respective bunt class:

Class 1, all heads smut free in 0 per cent class
Class 2, up to one-third of heads smutted in 20 per cent class
Class 3, one-third to two-thirds of heads smutted in 50 per cent class
Class 4, above two-thirds of heads smutted in 80 per cent class
Class 5, all heads smutted in 100 per cent class

The plants in Class 1 were not pulled but were left in the field until maturity in order to make individual plant selections should any of them prove highly resistant to all four bunt forms. None, however, were resistant; consequently, no plant selections were made. The percentage of bunt was calculated according to the following illustration: Row 44 had nine smut-free plants, one 20 per cent plant, two 50 per cent plants, two 80 per cent plants, and three 100 per cent plants.

$$\frac{(1 \times 20) + (2 \times 50) + (2 \times 80) + (3 \times 100)}{17 \text{ (total number of plants)}} = 34 \text{ per cent bunt}$$

This method, in addition to giving the total per cent of bunt in the whole family, maintains the individual plant as the unit. The calculations were made to the nearest decimal place in percentages less than 10 and to the nearest whole number in those above 10.

Table 2. Distribution of Parents and F_3 Progenies into Bunt Classes When Inoculated with Four Physiologic Forms

Parents and F_3 progenies	Bunt form	Number of rows in each class															Total No. of rows	Average per cent bunt
		0	t - 1	1.1 - 3	3.1 - 6	6.1 - 10	11-15	16-21	22-28	29-36	37-45	46-55	56-66	67-78	79-91	92-100		
Albit	T-1	8															8	0.0
Minhardi										1	1	2	3	7	1		15	63.6
F_3		26	1		3	6	4	6	2	2	2	1	2		2		57	12.4
Albit	1-5	10															10	0.0
Minhardi														4	10		14	80.2
F_3		35			2	6	5	11	13	9	3	3	5	8	3	1	104	23.6
Albit	T-13												1	1	4		6	73.6
Minhardi														1	10	2	13	86.9
F_3												1	4	17	40	18	80	82.6
Albit	T-2												1	4	6		11	80.0
Minhardi															9	3	12	89.9
F_3													3	28	46	12	89	81.8

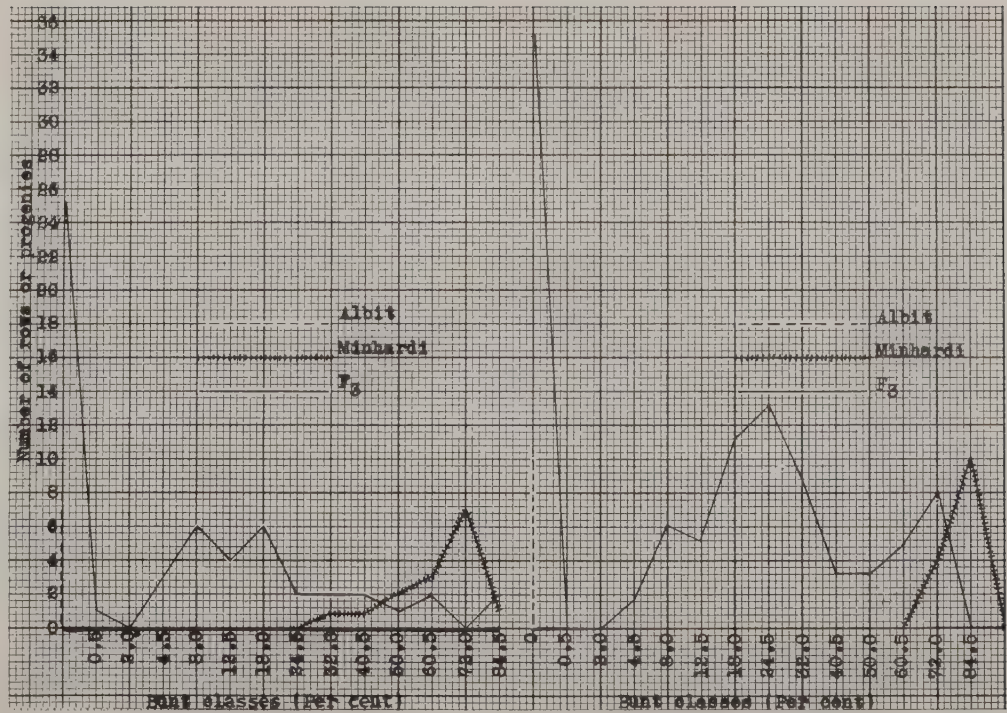

Fig. 1. Distribution of parents and F_3 families in per cent bunt classes. Inoculum T-1.

Fig. 2. Distribution of parents and F_3 families in per cent bunt classes. Inoculum L-5.

In the final analysis of the F_3 progeny for bunt resistance only rows with 15 or more plants were used, this number being chosen quite arbitrarily. It should be stated here that there was some volunteer wheat which was rogued wherever possible. However, there were three rows that had one or two plants that were somewhat similar to the *vulgare* segregates of the Albit x Minhardi cross that were not rogued. These plants were eliminated later on account of a very unusual segregation.

EXPERIMENTAL RESULTS

Albit x Minhardi

Reaction to T-1, T-2, T-13, and L-5. The cross was made in 1929. The F_1 and F_2 populations were grown the two following years. The inheritance of bunt resistance of an F_2 family was studied on the basis of the breeding behavior of the F_3 progeny.

The distribution into bunt classes of parents and F_3 progenies for four forms is shown in Table 2, and for forms T-1 and L-5 is shown graphically in Figures 1 and 2. The size of the bunt classes in Table 2 agrees with those used by Smith (40). The minima in the curves indicate the divisions of the different F_2 plants into their respective phenotypes. Recently Briggs (10) demonstrated that the minima in the curve indicate the division between phenotypes quite accurately. Such a division was made in Figure 1 with the exception that the smut-free group was placed on zero per cent smut, as in the resistant parent, rather than on two per cent. The other two minima fall on 12.5 and 50 per cent. When these divisions are made, the number of families in each group is as follows:

26 smut free
12 intermediate resistant
15 intermediate susceptible
4 susceptible

The numerical distribution of these four groups suggests a 7:4:4:1 ratio that can be explained on the basis of two main factors either one of which confers immunity. According to Fisher (15), this ratio is very close to the theoretical ratio as shown in Table 3. P yields the highly significant value of .93, which means that 93 times out of 100 as poor an agreement might be expected from chance alone.

By observing Figures 1 and 2, it can be seen that there is some similarity in the two curves. Both curves show the presence of a large number of smut-free families with a larger number of intermediate families and a comparatively small number of susceptible families. However, in Figure 1, the intermediate families can be divided into two groups of approximately equal value, whereas in

Table 3. Test for Goodness of Fit of Albit x Minhardi F_3 for a 7:4:4:1 Ratio for Smut Resistance When Inoculated with T-1

Observed	Calculated	O-C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
26	24.93 (7)	1.07	1.1449	.0459
12	14.25 (4)	2.25	5.0625	.3552
15	14.25 (4)	0.75	0.5625	.0394
4	3.57 (1)	0.43	0.1849	.0517

$X^2 = .492$ $P = .93$

Figure 2 the number of intermediate susceptible families far exceed those of the intermediate resistant families. Also Figure 2 shows a larger number of susceptible families than Figure 1 which brings out the greater virulence of L-5. The relationship between the bunt forms, T-1 and L-5, can best be seen in Table 4, in which appears a correlation surface between smut forms T-1 and L-5 in 48 progenies of each of two portions of Albit x Minhardi F_3. The correlation coeffcient r equals $.956 \pm .008$. It can also be seen that there are three well defined groups in the correlation surface. Now, if all the frequencies except those in the two homozygous groups, i.e., all those not of the composition $A^1A^1A^2A^2$ and $a^1a^1a^2a^2$, are considered as the intermediate group, the observed as well as the calculated ratio is 7:8:1. Because of the close relationship between these two forms, we are compelled to assume that the same two main factors that govern resistance to T-1 are also responsible for resistance to L-5. This, however, does not account for all of the facts since when application of the same numerical distribution, viz., 7:8(4:4):1, that was taken for the reaction to T-1 is made for the reaction to L-5, a rather unsatisfactory fit results When the minima in Figure 2 are taken as the points of division between groups, the number in each class is as follows:

35 smut free
10 intermediate resistant
47 intermediate susceptible
12 susceptible

It is assumed that an inhibiting factor, I, is introduced by Minhardi which has no effect against T-1. In this hypothesis it is assumed that factor I inhibits the action of A^1 but not of A^2. On the basis of this assumption, the theoretical number in each group is:

30.9 smut free
13.0 intermediate resistant
48.7 intermediate susceptible
11.4 susceptible

Table 4. Correlation between Smut Forms T-1 and L-5 in 48 Progenies of Each of Two Portions of Albit x Minhardi F_3

T-1		L-5: A^2A^2						A^2a^2								a^2a^2	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
A^1A^1	1	21							1								22
	2	1															1
	3																0
	4	2			1	1			1								5
	5					1		1		1	1						4
	6						2				1						3
A^1a^1	7						1	2	1				1				5
	8							1									1
	9									1				1			2
	10											1					1
	11												1				1
	12														1		1
	13																0
a^1a^1	14													1		1	2
	15																0
		24	0	0	1	2	3	4	3	2	2	1	2	2	1	1	48

$r = .956 \pm .008$ $P = 1.00$ for 7:8:1 ratio

For this ratio, P has a value of .72, indicating a good fit. Albit, the resistant parent, can be designated as $A^1A^1A^2A^2ii$ and Minhardi as $a^1a^1a^2a^2II$. The F_2 would then segregate as follows:

		Reaction to T-1	Reaction to L-5
1	$A^1A^1A^2A^2II$	Smut free	Smut free
2	$A^1A^1A^2A^2Ii$	Smut free	Smut free
1	$A^1A^1A^2A^2ii$	Smut free	Smut free
2	$A^1A^1A^2a^2II$	Smut free	Intermediate susceptible
4	$A^1A^1A^2a^2Ii$	Smut free	Intermediate resistant
2	$A^1A^1A^2a^2ii$	Smut free	Smut free
1	$A^1A^1a^2a^2II$	Smut free	Susceptible
2	$A^1A^1a^2a^2Ii$	Smut free	Intermediate susceptible
1	$A^1A^1a^2a^2ii$	Smut free	Smut free
2	$A^1a^1A^2A^2II$	Smut free	Smut free
4	$A^1a^1A^2A^2Ii$	Smut free	Smut free
2	$A^1a^1A^2A^2ii$	Smut free	Smut free
4	$A^1a^1A^2a^2II$	Intermediate resistant	Intermediate susceptible
8	$A^1a^1A^2a^2Ii$	Intermediate resistant	Intermediate susceptible
4	$A^1a^1A^2a^2ii$	Intermediate resistant	Intermediate resistant
2	$A^1a^1a^2a^2II$	Intermediate susceptible	Susceptible
4	$A^1a^1a^2a^2Ii$	Intermediate susceptible	Intermediate susceptible
2	$A^1a^1a^2a^2ii$	Intermediate susceptible	Intermediate susceptible
1	$a^1a^1A^2A^2II$	Smut free	Smut free
2	$a^1a^1A^2A^2Ii$	Smut free	Smut free
1	$a^1a^1A^2A^2ii$	Smut free	Smut free
2	$a^1a^1A^2a^2II$	Intermediate susceptible	Intermediate susceptible
4	$a^1a^1A^2a^2Ii$	Intermediate susceptible	Intermediate susceptible
2	$a^1a^1A^2a^2ii$	Intermediate susceptible	Intermediate susceptible
1	$a^1a^1a^2a^2II$	Susceptible	Susceptible
2	$a^1a^1a^2a^2Ii$	Susceptible	Susceptible
1	$a^1a^1a^2a^2ii$	Susceptible	Susceptible

A comparison of the per cent bunt from infection by T-1 and L_r-5 on the 48 Albit x Minhardi F_3, which appears on the correlation surface (Table 4), is made in Table 5. On the basis of the above-mentioned hypothesis, nine phenotypic classes should appear:

Group 1 Smut free to both forms

Group 2 Smut free to T-1, intermediate resistant (trace to 14% smut) to L_r-5

Group 3 Smut free to T-1, intermediate susceptible (15 to 66%) to L_r-5

Group 4 Smut free to T-1, susceptible (67 to 100%) to L_r-5

Group 5 Intermediate resistant to T-1 (trace to 15%), intermediate resistant to L_r-5

Group 6 Intermediate resistant to T-1, intermediate susceptible to L_r-5

Group 7 Intermediate susceptible (16 to 55%) to T-1, intermediate susceptible to L_r-5

Group 8 Intermediate susceptible to T-1, susceptible to L_r-5

Group 9 Susceptible to both forms

In Table 5 all groups except 2 and 4 appear; this, however, is not a serious deviation considering the low number (48) of families in the test.

Neither Albit nor Minhardi possess genes for resistance to T-13 and T-2 or, if any, they are only minor factors.

Table 5. Comparison of Per Cent Bunt on Albit x Minhardi F_3 to Bunt Forms T-1 and L-5, and probable Genetic Constitution of the F_3 Families Arranged in Order of Groups with Ascending Smut Percentages

Number of families	Per cent bunt		Group	Probable genetic constitution of F_2
	T-1	L-5		
22	0	0	1	Progenies in group 1 include the following genotypes: $A^1A^1A^2A^2II$, $A^1A^1A^2A^2Ii$, $A^1A^1A^2A^2ii$, $A^1A^1A^2a^2ii$, $A^1A^1a^2a^2ii$, $A^1a^1A^2A^2II$, $A^1a^1A^2A^2Ii$, $A^1a^1A^2A^2ii$, $a^1a^1A^2A^2II$, $a^1a^1A^2A^2Ii$, $a^1a^1A^2A^2ii$
1	0	22	3	$A^1A^1A^2a^2II$
2	6	0	5	$A^1a^1A^2a^2ii$
1	6	6	5	$A^1a^1A^2a^2ii$
1	5	8	5	$A^1a^1A^2a^2ii$
1	7	8	5	$A^1a^1A^2a^2ii$
1	13	13	5	$A^1a^1A^2a^2ii$
1	13	14	5	$A^1a^1A^2a^2Ii$
1	7	19	6	$A^1a^1A^2a^2Ii$
1	8	33	6	$A^1a^1A^2a^2Ii$
1	6	25	6	$A^1a^1A^2a^2Ii$
1	7	41	6	$A^1a^1A^2a^2II$
1	19	18	7	$A^1a^1a^2a^2ii$
1	21	23	7	$A^1a^1a^2a^2ii$
1	18	13	7	$A^1a^1a^2a^2ii$
1	20	18	7	$A^1a^1a^2a^2ii$
1	22	20	7	$A^1a^1a^2a^2ii$
1	33	29	7	$A^1a^1a^2a^2ii$
1	46	61	7	$A^1a^1a^2a^2Ii$
1	17	66	7	$A^1a^1a^2a^2Ii$
1	15	41	7	$A^1a^1a^2a^2Ii$
1	40	47	7	$A^1a^1a^2a^2Ii$
1	34	76	8	$A^1a^1a^2a^2II$
1	65	83	9	$a^1a^1a^2a^2II(Ii)$ or (ii)
1	87	76	9	$a^1a^1a^2a^2II(Ii)$ or (ii)
1	79	93	9	$a^1a^1a^2a^2II(Ii)$ or (ii)

Table 6. Distribution of Parents and F_3 Progenies into Bunt Classes When Inoculated with Four Physiologic Forms of Bunt

Parent and F_3 progenies	Bunt form	Number of rows in each bunt class															Total No. of rows	Average per cent bunt
		0	t-1	1.1 - 3	3.1 - 6	6.1 - 10	11 - 15	16 - 21	22 - 28	29 - 36	37 - 45	46 - 55	56 - 66	67 - 78	79 - 91	92 - 100		
Albit	T-1	7															7	0.0
Buffum 17								2	2		4	2					10	34.4
F_3		8	1		4	7	7	6	8	3	6	5	5	1	1		62	24.5
Albit	L-5	9															9	0.0
Buffum 17										1		2	3	5			11	60.2
F_3		11			1	11	6	10	10	6	2	2	8	6	10	1	84	33.1
Albit	T-13												1	1	4		6	76.3
Buffum 17												1	3	3	1	1	9	70.5
F_3												3	2	5	12	6	28	80.1
Albit	T-2												1	4	6		11	80.0
Buffum 17											1		2	6			9	68.8
F_3												1	2	10	29	14	56	83.4

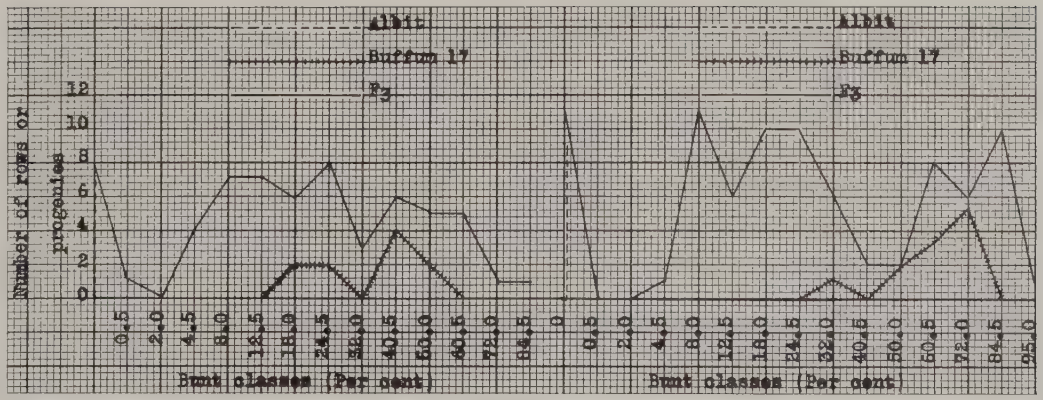

Fig. 3. Distribution of parents and F_3 families in per cent bunt classes. Inoculum T-1.

Fig. 4. Distribution of parents and F_3 families in per cent bunt classes. Inoculum L-5.

Albit x Buffum 17

Reaction to T-1, T-2, T-13, and L-5. The distribution of parents and F_3 into bunt classes for the four forms is shown in Table 6 and for forms T-1 and L-5 is shown graphically in Figures 3 and 4. The low number of families—62 for T-1 and 84 for L-5—prevents a satisfactory analysis.

The appearance of segregates that are more susceptible than the susceptible parent suggests that a factor for resistance is carried by

Table 7. Correlation between Smut Forms T-1 and L-5 in 53 Progenies of Each of Two Portions of Albit x Buffum 17 F_3

T-1 \ L-5	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1	5			1												6
2																0
3																0
4	1				1		1									3
5					1	2	1	1	1							6
6					2		2	1								5
7	1					2	1	1								5
8						1	4	3		1						9
9					1								1			2
10					1							2	2	1		6
11										1		1	1	1	1	5
12										1		1	1	1		4
13													1			1
14														1		1
15																0
	7	0	0	1	6	5	9	6	1	3	0	4	6	4	1	53

$r = .855 \pm .003$

Buffum 17 which reduces the amount of smut from complete susceptibility (70 to 90 per cent on some of the F_3 families) to 34 per cent by T-1 and to 60 per cent by L-5. When this factor is recessive and combined with the recessives a^1 and a^2, it results in completely susceptible progenies exceeding the limits of the parents with each form of smut. The low number of smut-free segregates as compared with the susceptible types shows that three factors do not account for all of the facts. It is thought that Buffum 17 introduces an inhibiting factor, Ib, which prevents the action of both factors carried by Albit.

There is a striking similarity in Figures 3 and 4. This similarity or relationship is shown in the correlation surface, Table 7, in which r is $.855 \pm .003$ indicating that the genes for resistance to T-1 and L-5 possess a relationship in Albit x Buffum 17 similar to that found in Albit x Minhardi.

Spike Density. The method of measurement consisted of measuring 10 rachis internodes approximately in the center of the best developed head of a single plant.

The frequency distribution of spike-density of parents and F_2 of both crosses and of Albit x Minhardi F_3 progenies into classes is shown in Table 8. In 1931 the spike-density of Albit ranged from 18 to 22 millimeters with a mean of 20 mm.; Minhardi ranged from 46 to 56 mm., mean 50.5; Buffum 17 ranged from 52 to 60 mm., mean 55.8. The 301 F_2 families of Albit x Minhardi ranged from the shortest dense parent to one class longer than the lax parent—none was found in the intermediate class 38. In the Albit x Buffum 17 F_2 the extremes of the parents were obtained but no progenies were found with the mean spike-densities of 38 and 42 millimeters. The distribution into spike-density classes for the F_2 and F_3 progenies is shown graphically in Figure 5. When the minima in the curves are taken as the points of division between groups, the observed number compared with the calculated in each group is as follows:

	Observed	Calculated (3:1)	O - C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Albit x Minhardi F_2					
Club	234	225.75	8.25	68.0625	.301
Lax	67	75.25	8.25	68.0625	.904
Total	301	301.00			$X^2 = 1.205$
					$P = .28$
Albit x Buffum 17 F_2					
Club	157	151.5	5.5	30.25	.1996
Lax	45	50.5	5.5	30.25	.5990
Total	202	202.0			$X^2 = .7986$
					$P = .39$

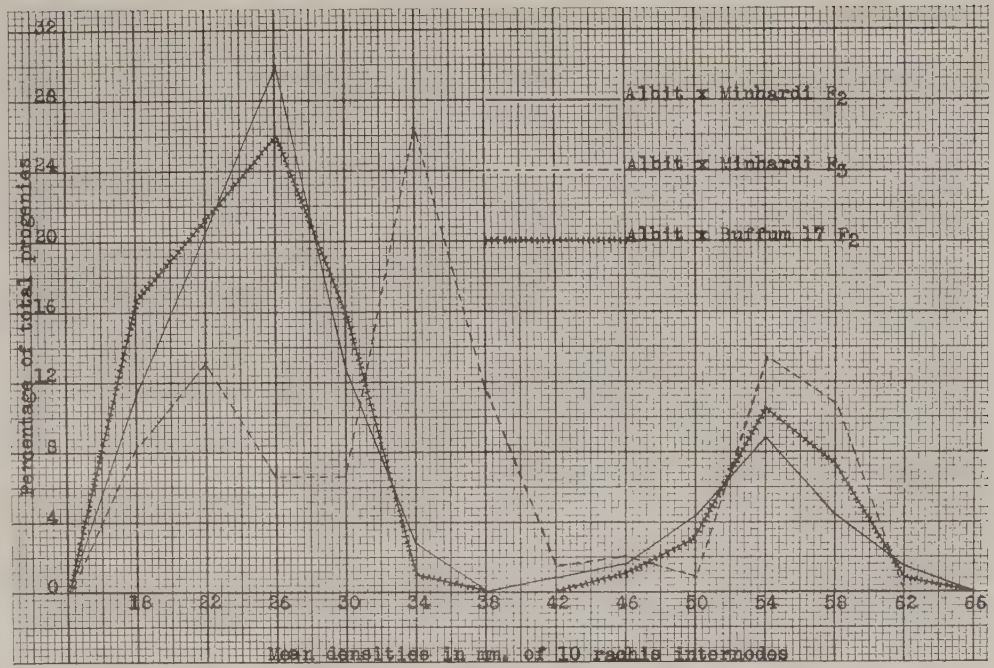

Fig. 5. Spike-density curves of F_2 and F_3 progenies of Albit x Minhardi and of F_2 progenies of Albit x Buffum 17.

Table 8. Frequency Distribution of Spike Density of Parents of F_2 Progenies of Albit x Minhardi and Albit x Buffum 17, and F_3 Progenies of Albit x Minhardi

Cross or variety and year	10 rachis internodes in millimeters												Total
	18	22	26	30	34	38	42	46	50	54	58	62	
Albit 1931	5	15											20
Albit 1932		5	4										9
Minhardi 1931								3	10	5	2		20
Minhardi 1932									1	9			10
Buffum 17 1931										13	5	2	20
A x M F_2 1931	35	62	88	41	8		2	5	13	27	14	6	301
A x M F_3 1932	8	13	6	6	26	10	1	2	1	13	9		95
A x B F_2 1931	34	37	53	32	1			1	6	21	15	2	202

These numbers were subjected to a test for goodness of fit to a 3:1 ratio according to Fisher (15). P in each case—.28 for Albit x Minhardi and .39 for Albit x Buffum 17—yields values that indicate spike-density in both crosses is due to a single main factor. The F_3 progenies of Albit x Minhardi were subjected to a similar test the following year. Of these, 95 families were studied for spike-density. The best developed head from each F_3 plant was measured and from it the mean, standard deviation, and coefficient of variability were calculated. Three well-defined groups are clearly indicated in Figure 5 in which the distribution results in a tri-modal curve. On the basis of this curve, again using the minima as the points of division between groups, the observed number compared with the calculated for a 1:2:1 ratio is as follows:

	Observed	Calculated (1:2:1)	O - C	$(O-C)^2$	$\frac{(O-C)^2}{C}$
Club	27.00	23.75	3.25	10.5625	.444
Intermediate	43.00	47.50	4.50	20.2500	.426
Lax	25.00	23.75	1.25	1.5625	.066
Total	95.00	95.00			

$$X^2 = .936$$
$$P = .513$$

In this comparison P = .51. When the 95 F_3 families are placed into spike-density classes according to their range in coefficient of variability (C. V. classes), Table 9, a slightly different picture is seen.

Table 9. Mean Spike-Density and Coefficient of Variability (C. V.) Classes of Albit x Minhardi F_3. Length in Millimeters of 10 Rachis Internodes Measured in Center of Head

C. V. classes	Spike-density class centers												Total
	18	22	26	30	34	38	42	46	50	54	58	62	
6	2	2						1		1			6
10	6	7						1		11	8		33
14		4	1						1	1	1		8
18													0
22													0
26													0
30				1									1
34			1		3	1							5
38			2	2	3	3							13
42			1	2	7	2	1						13
46				1	8	3							12
50			1		2	1							4
	8	13	6	6	26	10	1	2	1	13	9	0	95

When the data in the curve are analyzed, all the progenies in the mean spike-densities of 18, 22, and 26 mm. were considered in the homozygous group. The data presented in Table 9, however, show that this is not the correct analysis, since five of those considered in the homozygous club types have a coefficient of variability greatly exceeding that of the club parent. The number in each group is changed from 27:43:25 to 22:48:25 to correspond with the C. V. classes. This change makes a better fit for the expected 1:2:1 ratio.

From the above illustration it is apparent that data which are being analyzed should be subjected to various "statistical tools" before a final interpretation is made.

Seed Color. All the F_1 plants were red seeded. Of the 301 F_2 progenies of Albit x Minhardi, there were 280 red-seeded and 21 white-seeded; 202 Albit x Buffum 17 F_2 progenies segregated into 190 red: 12 white. The results in both crosses indicate a two-factor difference, giving approximately a 15 : 1 ratio. One hundred and fourteen Albit x Minhardi F_3 progenies were studied for seed color the following year (1932). Seven white-seeded plants bred true for white in the F_3; 67 bred true for red; 23 segregated 3 red : 1 white; and, 17 segregated

15 red : 1 white. It was thought advisable to test the observed numbers of red and white seeded plants with the expected numbers. This was done as described by Harrington and Smith (27). In Fisher's (15) X^2 table, *n* has not been calculated beyond 30. The number of degrees of freedom is 39. Fisher states that a good approximation is given by assuming that $(\sqrt{2X^2} - \sqrt{2n - 1})$ is normally distributed about zero with unit standard deviation. He suggests further that if this quantity is materially greater than two, the value of X^2 is not in accordance with expectation. In this comparison $X^2 = 34.8$; substituting in the formula $(\sqrt{2X^2} - \sqrt{2n - 1})$, we have $(\sqrt{69.6} - \sqrt{78 - 1})$ or $-.43$. Consequently, it can be assumed that the classification into the 3:1 and 15:1 ratios is correct.

Bunt Reaction as Related to Other Plant Characters

The tendency of certain traits to remain together in inheritance, i.e., linkage, has been studied in great detail in certain phases of genetics. T. H. Morgan's work with Drosophila is of special interest in this field, and many linkage studies have been made with crop plants. Hayes and Garber (28) cite a number of investigators, among whom are Biffen, Engledow, Gaines and Carstens, and others who have reported cases of linkage in wheat crosses.

In any wheat-breeding program where a number of desirable qualities are being sought, it is always of interest and often of value to the plant breeder with a strictly utilitarian viewpoint to know whether any one character is linked with any other.

In this study, the data on the two characters, spike-density and color of grain, are compared with the data on smut resistance in order to determine whether or not there was any linkage between the factors controlling these various characters (Tables 10 and 11).

Table 10. A Comparison of Smut Resistance to T-1 with Spike-Density in F_3 Progenies of Albit x Minhardi

Group	Spike-density class centers											Total	Mean
	18	22	26	30	34	38	42	46	50	54	58		
Smut free	2	1	2		5	1				3	2	16	37.25
Intermediate	1	2		3	3	2				2	3	16	38.25
Susceptible	1					1			1	1		4	40.00
Total	4	3	2	3	8	4	0	0	1	6	5	36	

A comparison of the data on smut resistance to physiologic form T-1 with the data on spike-density in the F_3 progenies of Albit x Minhardi (Table 10) indicates that there is little, if any, relationship

Table 11. A Comparison of Smut Resistance to T-1 with Seed Color in F_3 Progenies of Albit x Minhardi

Group	Smut group			Total
	Smut free	Intermediate	Susceptible	
Pure red	10	8	2	20
Segregating 3:1	3	4		7
Segregating 15:1	3	3	2	8
Pure white	3	1		4
	19	16	4	39

between these two characters since the three groups, smut-free, intermediate, and susceptible progenies, are not confined to any particular spike-density class, but are distributed promiscuously through the various classes, although the mean spike-density is 2.75 units less for the smut-free than for the susceptible classes.

The high value of r, $.956 \pm .008$, between the two portions of F_2 seed inoculated with the two forms T-1 and L-5 suggests that a similar relationship would be found if spike-density were correlated with reaction to the latter form in this particular cross.

A comparison of smut resistance and seed color in the F_3 progenies of Albit x Minhardi is shown in Table 11. Albit, white-seeded, is the resistant parent and yet, of the 20 pure red-seeded F_3 progenies, 10 are smut free. No susceptible pure white progenies were discovered; however, the number (4) of pure whites is so low that it is impossible to draw any satisfactory conclusion concerning this particular group. The nature of the distribution of the four groups, viz., pure reds, those segregating 3:1, those segregating 15:1, and pure whites, into the three smut groups—smut free, intermediate, and susceptible—indicates a possible linkage between smut resistance to T-1 and seed color as the pure whites and 3:1 segregates have no susceptible classes while the other two classes have four.

DISCUSSION

In the present study of inheritance of bunt resistance it was definitely shown that the particular smut biotype used as inoculum may be as much an influencing factor as the variety of wheat in determining the number of factors governing resistance. What may at first seem to be conflicting results of investigators working at different stations with similar varieties of wheat, may be that they have worked with different biotypes of smut. At the Washington Agricultural

Experiment Station at Pullman, Washington, all biotypes are numbered and their purity is maintained by culturing them on differential host testers. Table 1 illustrates the types of varieties used in differentiating the smut forms T-1, L-5, T-2, and T-13 used in this work.

Data are presented on F_3 progenies of two winter wheat crosses that are completely susceptible when inoculated with forms T-13 and T-2 to which both parents are susceptible, but a series ranging from immunity to complete susceptibility is found in the F_3 progenies when inoculated with forms T-1 and L-5 to which one parent is immune and the other susceptible. It shows that two factors for resistance to one form do not necessarily confer resistance to another bunt form.

The part that certain environmental factors play in a study of this type has been described. Both Hungerford (33) and Smith (41) have demonstrated that temperature is an influencing factor. Hungerford concluded that low soil temperatures and a fairly high percentage of moisture in the soil are both conducive to stinking smut infection. Smith (41) in a somewhat similar study analyzed the relation between temperature and reaction to bunt at different stages of growth for Hope and Jenkin in the greenhouse. Hope was resistant when grown at a relatively low temperature until emergence from the soil and then grown at a higher temperature, although Jenkin was susceptible. Hope grown continuously in the cool environment was quite susceptible, as was Jenkin.

Woolman (55) states, "the fungus enters seedlings of both resistant and susceptible varieties with equal facility, but, in the most resistant varieties studied, apparently it does not develop beyond the first phase, except in rare cases." Woolman describes the first phase as the entrance of the hypha into and its development within the epidermal cell, in which phase it is gram-negative and both intercellular and intracellular. Microscopic observations made by the author have revealed that the fungus is present in the outer epidermis of the coleoptile in both the resistant and susceptible parents.

Varieties of wheat apparently similar in appearance may manifest entirely different reactions to smut. The average per cent bunt of Buffum 17 was 34.4 when inoculated with T-1 and 60.2 when inoculated with L-5 (Table 6) as compared with 63.6 and 80.2 respectively for Minhardi (Table 2). Yet the average per cent bunt of the Albit x Minhardi F_3 progeny is considerably lower than for the F_3 progeny of Albit x Buffum 17. The nature of the distribution into bunt classes of the F_3 families indicates that Buffum 17 possesses a gene complex for resistance that is quite different from that of Minhardi. On account of the low number of families in the Albit x Buffum 17 cross, it was impossible to determine this difference with exactness.

Resistance to bunt has been interpreted as resulting from one, two, and multiple factors in different crosses. Briggs (5, 6, 7, 8, 9, 10) and Churchward (11, 12) both found resistance controlled by one factor. On the other hand, Gaines (21, 22) Gieseke (26), Knorr (34), and Aamodt (1) found more than one factor in all crosses studied. In the present study two main factors were found to be responsible for resistance in Albit x Minhardi to physiologic form T-1. These two main factors and an additional factor, an inhibitor, were found to govern resistance in the Albit x Minhardi cross to L-5 which is closely related to T-1 in physiological reactions in this particular cross.

SUMMARY

Data are presented on the reaction of three winter wheats and the F_3 progeny of two crosses to four biotypes of bunt.

The F_3 progeny of both crosses are completely susceptible when inoculated with forms T-13 and T-2 to which both parents are susceptible, but a series ranging from immunity to complete susceptibility is found in the F_3 when inoculated with forms T-1 and L-5 to which Albit is immune and Minhardi and Buffum 17 are susceptible.

In the F_3 generation of the Albit x Minhardi cross the four classes, smut-free, intermediate resistant, intermediate susceptible, and susceptible, gave a close approximation to a 7:4:4:1 ratio to form T-1. The results indicate a two-main-factor difference.

The coefficient of correlation between T-1 and L-5 ($r = .956 \pm .008$) indicates that the same two main factors responsible for resistance to form T-1 are also responsible for resistance to L-5. Minhardi introduces a factor which inhibits the action of A^1 against L-5 but not against T-1.

Neither Albit, Minhardi, nor Buffum 17 possess genes for resistance to forms T-13 and T-2.

Segregates more susceptible than Buffum 17 were found. It is possible that Buffum 17 carries a factor C which reduces the amount of bunt and an additional factor Ib which inhibits the action of both A^1 and A^2.

In the latter part of the paper, data are presented on inheritance of spike-density and seed color in Albit x Minhardi and Albit x Buffum 17.

Albit, the dense parent, varied in spike-density from 18 to 26 millimeters with a mean of 22 mm. of 10 rachis internodes measured in the center of the head; Minhardi ranged from 46 to 58 mm. with a mean of 50.5; Buffum 17 ranged from 52 to 60 mm., with a mean of 55.8. The Albit x Minhardi F_2 segregated into 234 club : 67 lax,

whereas 225.75 : 75.25 were expected on the basis of a 3:1 ratio. P = .28 in the comparison of observed and calculated numbers. In the Albit x Buffum 17 cross, spike-density can similarly be explained on a single-factor difference.

Minhardi and Buffum 17 each carry two dominant factors for red seed color. The Albit x Minhardi F_2 segregated into 190 red : 12 white. The F_3 progenies segregated into 67 pure red-seeded, 17 segregating 15:1, 23 segregating 3:1, and 7 pure white.

A comparison of the data on bunt reaction, spike-density, and seed color indicates a possible weak linkage between smut resistance to T-1 and spike-density and also between T-1 reaction and seed color.

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